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POLLINATOR SERVICE IN SYMPATRIC SPECIES OF JEWELWEED (*IMPATIENS*: BALSAMINACEAE)

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Since the 18th century biologists have been interested in the angiosperm flower as a mechanism for attracting insects and other agents to mediate sexual reproduction (Miller, 1724; Dobbs, 1750; Sprengel, 1793). In many obligate outcrosses seed production is solely dependent upon those insects responsible for proper transfer. If the number of pollinators is insufficient with respect to the number of self-incompatible flowers present, then the flowering species may be competing for limited pollinator services.

The consequences of interspecific competition for pollinator service by the honey bee has been a recognized economic problem for both apple and pear production in the presence of the more attractive white mustard, storkbill, and dandelion (Free, 1968, 1970). The pollinator services of the honey bee on alfalfa flowers are reportedly preempted by field crops of red clover, sweet clover, mustard and sunflowers (Hobbs, 1950; Menke, 1954; Palmer-Jones and Forster, 1965). Competition for pollinators in natural ecosystems has been noted in sympatric and synchronic species in the arctic and north temperate latitudes during the growing season (Hocking, 1968; Mosquin, 1971). Competition for pollinator service has received theoretical attention by several workers who have developed models to predict the outcome of competitive interactions on the basis of pollinator movement, pollinator constancy, flower density, etc. (Levin and Anderson, 1970; Straw, 1972). Yet the prevalence of competition for pollinator service and its relative importance as an organizing influence on interspecific interactions have not been ascertained.

As part of a more general study of plants and their pollinators, I selected to assess the competitive interactions between two species of jewelweed (*Impatiens*) which occur predominantly in separate patches along the flood plain of White Clay Creek in northern Delaware, but which occasionally are found growing together. It was assumed that if competition for pollinators were operating, it would become apparent in a comparison of plant-pollinator interactions between single-species and mixed-species patches. In addition to their microdistributional patterns these two species proved ideally suited to a competitive study for the following reasons: 1. they have similar floral structures and bloom synchronically, 2. they are completely dependent on the activities of pollinators for their reproduction, 3. they share pollinators, 4. they have a deficiency of pollinators relative to the number of flowers present as measured by the lack of 100% seed set.

Table 1. Floral characteristics and phenologies of *Impatiens capensis* and *Impatiens pallida* presented as means and standard deviations and sample size.

Characteristic	*I. capensis*	*I. pallida*
Saccate sepal length (mm)	18.2 ± 1.22 ($n = 35$)	10.4 ± 0.91 ($n = 25$)
Saccate sepal height (mm) (distance below androecium)	4.1 ± 0.43 ($n = 35$)	6.9 ± 0.42 ($n = 25$)
Spur length (mm)	8.6 ± 0.96 ($n = 35$)	5.2 ± 0.48 ($n = 25$)
Flower duration (days)	1.6 ± 0.63 ($n = 38$)	2.5 ± 0.86 ($n = 45$)
Androecium shed (days)	1.4 ± 0.52 ($n = 38$)	2.2 ± 0.84 ($n = 45$)
Nectar production (μl/24 h)	2.8 ± 1.61 ($n = 53$)	2.4 ± 1.56 ($n = 71$)
Nectar sugar (%)	43.1 ± 13.15 ($n = 43$)	41.5 ± 10.78 ($n = 24$)

Flowers

Flowers of the orange-flowered jewelweed (*Impatiens capensis*) and the yellow-flowered jewelweed (*I. pallida*) are single, pendant, perfect, zygomorphic, protandrous, superior and theoretically 5-merous. They have 2 small green upper sepals and an enlarged saccate sepal open in the front and spurred at the bottom. The petals consist of an upper which is broader than long and 2 lobed lateral petals (regarded as 2 united). The saccate sepal and petals are orange in *I. capensis* and yellow in *I. pallida.* In both species, the saccate sepal and petals are spotted in various degrees with red. The saccate sepal in *I. pallida* is shorter and abruptly bent downward as compared to *I. capensis* (Table 1). Flowers of the 2 species exhibit minor differences in UV reflectance-absorbance patterns. In *I. capensis*, both surfaces of the saccate sepal and the inner surface of the petals absorb UV light and the anthers reflect it, while in *I. pallida*, only the lower surfaces of the saccate sepal and the middle section of the 2 lobed petals and the anthers absorb UV light (Rust, 1977).

In both species the 5 stamens form a covering over the stigmatic surface until the androecium is pushed off by the elongation of the ovary, about 4–6 h before the flower drops from the receptacle (Table 1). The androecium protects the flower against self pollination. Nectar is produced in the spur of the saccate sepal and production begins just prior to anthesis. Daily accumulation in the saccate sepal amounted to approximately 2.5 μl per flower and the percent sugar averaged about 42% for both species (Table 1). Nectar amino acids were different in the 2 species. *Impatiens pallida* nectar contained 14 amino acids while *Impatiens capensis* nectar contained 24 amino acids of which 5 were in concentrations greater than 100 nmol/ml. *Impatiens capensis* nectar contained all of the amino acids of *I. pallida* except phosphoserine; *I. capensis* had an average of nearly twice the total amino acids per ml nectar than *I. pallida* (2.1 μmol/ml to 1.1 μmol/ml)

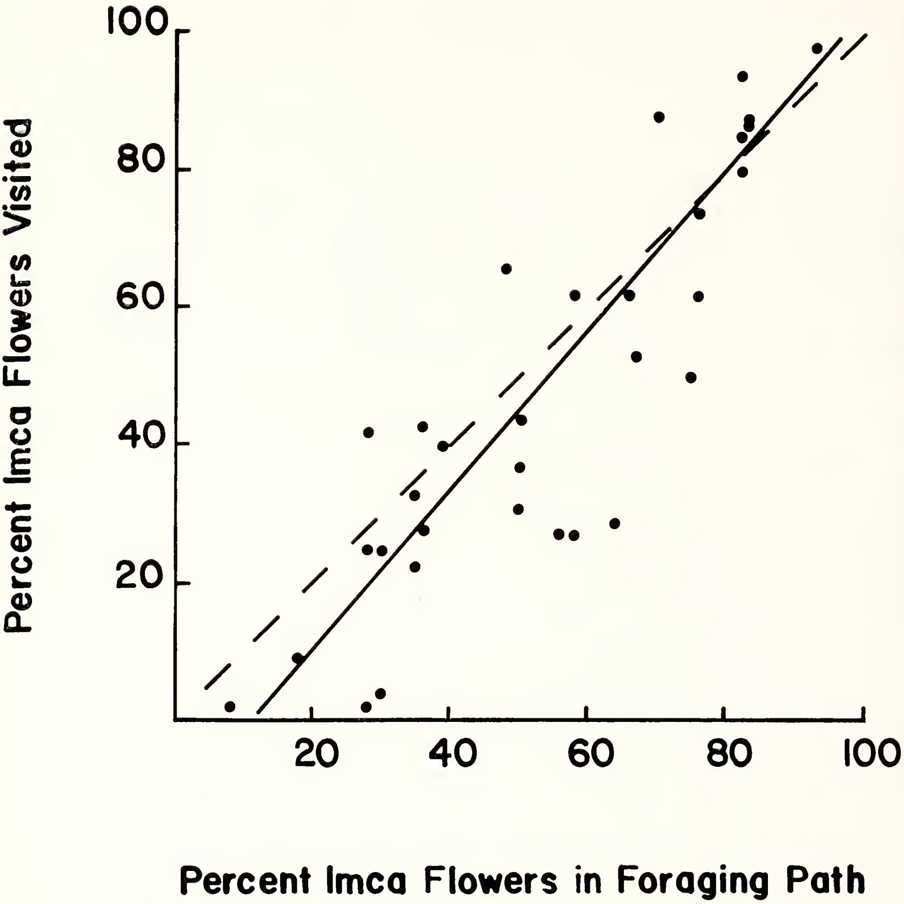

Fig. 1. Visitation pattern of *Bombus vagan* in mixed-species patches of *Impatiens capensis* and *Impatiens pallida* ($Y = 1.210X - 14.497$; $Ho{:}b = 1$, $0.05 < P < 0.10$). The dashed line equals the 1:1 relationship.

(Rust, 1977). However, the significance of different nectar compositions with respect to the attractiveness to pollinators has not been determined.

Pollinators and Flower-Pollinator Interactions

The 2 species shared the same principal pollinators, the bumblebees *Bombus vagans* and *B. impatiens.* Although other species were recorded visiting *Impatiens,* their numbers were relatively few. For this reason I restricted my behavioral observation to *B. vagans* and *B. impatiens.*

In an attempt to unravel the interspecific interactions, if any, as they related to pollinator service and to measure pollinator constancy and visita-

Table 2. Percentage of marked flowers of *Impatiens capensis* and *I. pallida* producing seeds in single- and mixed-species patches.

Date	*Impatiens capensis*		*Impatiens pallida*	
	alone	mixed	alone	mixed
21 August	81.4	87.1	91.6	93.3
28 August	76.7	83.3	75.0	100.0
4 September	65.7	77.7	70.0	84.5
11 September	74.0	83.8	54.5	86.1
18 September	57.1	40.0	75.0	81.8
Mean	70.9	74.3	73.2	89.1

tion rates, I followed an individual bee on a foraging trip through mixed-species and single-species patches recording the flowers visited and the time spent. Then I went back and counted the total number of flowers of each species in the foraging path and used these data to estimate the percentage of flowers of each species visited relative to their respective abundances. If there were no strong preference for or avoidance of either species by the pollinators, then I predicted that visitation should equal occurrence, i.e. the bees would have a low constancy.

Using *I. capensis* percentage of occurrence as the base, there was a significant increase in visitation when regressed against an increase in the percentage of *I. capensis* in a mixed-species patch (Fig. 1). In fact, the slope of the regression approached unity ($b = 1$), the perfect 1:1 relationship shown as the dashed line in Fig. 1. This means that as the percentage of *I. capensis* increased or decreased in a mixed patch, the visitation increased or decreased proportionately. *Bombus vagans* showed no constancy for one *Impatiens* species over the other. Insufficient numbers of *B. impatiens* have been timed to permit analysis. However, they appear to exhibit the same low level of constancy. Thus, the species' floral displays and rewards appear to be equally attractive to the principal pollinators. The bees do not respond to the differences between the *Impatiens* species, but move from flower to flower with a frequency proportional to the occurrence.

A comparison of visitation rates by pollinators was made to determine whether or not the lack of constancy affected these rates and hence the number of flowers pollinated in mixed-species patches. The rate of flowers visited by *Bombus vagans* averaged 8.4 ± 2.3/minute in *I. capensis* patches, 12.7 ± 3.6/minute in *I. pallida* patches, and 10.5 ± 2.5/minute in mixed-species patches. This latter value is intermediate and thus suggests that visitation rates are not significantly affected in mixed-species patches.

The second measurement of competition for pollinators involved marking flowers and following subsequent seed production. Individual flowers were marked with a 5 cm piece of size 40 cord tied around the pedicel. Approximately 50 flowers per week were marked in both mixed-species patches and single-species patches during each week throughout the flowering period. Marked, hand-pollinated flowers produced 100% seed set. For *I. capensis* there was no difference ($t = 0.461$, $P > 0.50$; based on arcsine transformation of the data) in pollination-seed production between mixed- and single-species patches (Table 2). However, *I. pallida* showed a significantly higher percentage of pollination-seed production in mixed-species patches ($t = 2.306$, $0.05 < P < 0.01$) (Table 2). It appears that *I. pallida* benefits from its association with *I. capensis* in terms of seed set, i.e. *I. pallida* exhibits facilitated pollination service in the presence of *I. capensis*. *I. capensis* neither benefits from nor is harmed by the presence of *I. pallida* with respect to seed production.

Conclusions

The fact that the two species of *Impatiens* were rarely found growing together, though both existed in the same general area, suggested that some form of competitive exclusion was taking place. Having obtained 100% seed set in both species through hand pollination and knowing seed set to be less than 100% in either species under natural conditions, it was concluded that pollinators may be limited and could be exerting a selective pressure on the species to become more "attractive" to the pollinators. However, constancy was not determined by the pollinators for one species of *Impatiens* over the other. There was an equal visitation in relation to the proportion of flowers of both species present. *Impatiens capensis* and *I. pallida* are not competing for pollinator service. Observations indicate that they are most likely competing at the level of seedling growth or perhaps seed survival.

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